VII. The effect of Oil of Citronella on two species of Dacus. By F. M. Howlett, B.A., F.E.S.

[Read February 7th, 1912.]

PLATES XXXIX, XL.

THE observations which form the subject of this paper were made in the course of work on fruit-flies at the Pusa Research Institute.

The common fruit-flies of Pusa are *Dacus diversus*, Coq., and *D. zonatus*, Saund. (*Rivellia persicae*, Big.). Of these the latter is a serious pest of peaches and mangoes, and like other fruit-flies it is a pest whose attacks are particu-

larly difficult to combat.

With the idea of attracting the females of zonatus to lay eggs, by imitating the smell of ripe peaches or mangoes, a large number of essential oils were experimented with. In the course of these experiments I heard that a neighbour had been troubled by some kind of fly settling on him at a time when he was using oil of citronella, sprinkled on his handkerchief, as a mosquito deterrent. Since the smell of this oil in no way resembles that of mangoes or peaches, its effect on Dacus had not been tried, but as soon as a handkerchief wetted with the oil was exposed in the neighbourhood of the peach-orchard it became evident that the smell exercised an extraordinarily powerful attraction. In less than half an hour the handkerchief, lying in a crumpled heap, was almost hidden by a crowd of D. zonatus, and presented a very striking appearance. I jumped at once to the conclusion that the economic problem of how to destroy female fruit-flies had found an easy solution, but on examination it was soon apparent that all the flies on the handkerchief were males; they almost refused to leave the neighbourhood of the handkerchief, and a considerable number of them followed me home when I removed it. A handkerchief was pinned to a sheet of cork and exposed in the peach-orchard for twenty minutes, the centre of the handkerchief being moistened with citronella. Plate XXXIX shows the male flies assembled. The cork sheet was then removed for

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a distance of about five yards and vigorously shaken and waved in the air to dislodge and disturb the flies; it was then replaced, and the flies which had returned to it are shown in Plate XL, which is a photograph taken exactly three minutes after its first removal, or perhaps two

minutes after it was replaced.

In both the photographs it will be noticed that the flies are congregated not actually on the moistened patch but round its margin. This is their usual custom, and was taken advantage of in catching the flies with fly-papers. If citronella is put in the middle of the fly-paper (on the gummy substance) many flies escape capture by sitting on the edge of the paper which is free of adhesive; if, instead of this, the citronella is put on the edge of the paper, they will not sit on it, but settle on the sticky surface: a very sensible difference is thus made in the number of flies Fly-papers treated with citronella were exposed in the orchard during the months of March, April, May and June. A careful estimate of the number caught during part of this period gave approximately eighteen thousand, and among these not more than fifty females were seen, or 0.3 per cent. Since the reaction was confined to the male sex and did not appear to be in any way connected with feeding habits, it seemed most reasonable to suppose that the smell might resemble some sexual odour of the female which in natural conditions served to guide the male to her.

Six or seven freshly killed females were therefore placed in a clean glass tube which was closed for about an hour with clean cotton-wool. On smelling the tube a faint odour resembling that of citronella was just perceptible, but although the presence of the smell was confirmed by my assistant, it was so faint that I feared the influence of unconscious "auto-suggestion" on our judgment, and repeated the experiment with about twenty living females which had emerged from the pupa from 6 to 24 hours previously. In this case the smell was distinctly perceptible and closely resembled the citronella smell; its presence and nature were confirmed by an independent observer who did not know what smell was being looked for or expected. When a similar number of males were tried in the same way, no smell of citronella

was detected.

It seems probable, therefore, that this smell is the

sexual attracting smell of D. zonatus. It is noteworthy that the oil also has an attraction for males of the species D. diversus, and a considerable number of them were caught on the fly-papers in March and April; the attraction in this case, however, seems to be perhaps a trifle less powerful than with zonatus, though it is difficult to be certain on the point. The number of diversus caught probably did not exceed 25 per cent. of the total of the two species, as towards the end of April diversus became scarce and zonatus very abundant up to the end of June. The quality of the oil affected the result, old oil being more effective than new; I have been unable to get analyses which would show wherein the difference lies. and what is the precise constituent which is of most importance. Some samples of eucalyptus oil seemed also to possess some slight attraction for zonatus males, but they never came to it in large numbers, nor did they come when there was any oil of citronella exposed in the neighbourhood. The distance at which the flies are able to perceive the smell of citronella is doubtful, but seems to be considerable; half a mile is probably not an extravagant estimate if the wind be favourable. By exposing a rag moistened with oil for half an hour or so in places where ordinary collecting fails to reveal the presence of a single fly, it is often possible to catch considerable numbers.

The smell is in all probability perceived by means of the antennae. To test this a rag wet with citronella was exposed, and of the visiting flies six or eight were caught and their antennae were carefully amputated at the base of the second joint; they were then liberated, seeming none the worse for the operation, and the rag was watched to see whether they again visited it. None of the flies operated on returned to the rag, though normally flies caught and liberated anywhere near such a rag will always return to it sooner or later, and generally quite quickly (cf. Plate XL). On one occasion a marked fly was driven away five times, but returned almost immediately after each repulse.

A curious fact is that the oil has an actually poisonous effect on the fly when the latter is exposed to its vapour in a fairly concentrated form, this effect being independent of the presence or absence of the antennae.

Four male zonatus were taken and the antennae of two of them were amputated; they were then confined in glass

vessels, each of the vessels containing a fragment of blotting-paper wetted with citronella oil. Four others similarly treated were confined in vessels without any citronella. The result was as follows:

With citronella. 2 amputated 3 put in 10.40 a.m., dead at 11.0.

2 normal 3 put in at 10.20 a.m., dead at 11.0.

Without citronella.

2 amputated 3 put in at 10.30 a.m., June 16th. Both lively 7.30 a.m., 17th. Both found dead at 7.0 a.m., 18th.

2 normal 3 put in at 10.25 a.m., 16th. One dead 7.30 a.m., 17th. Other

dead 7.0 a.m., 18th.

This poisonous action may account for the fact that the attractiveness of a rag is not proportional to the amount of citronella with which it is wetted, a rag thoroughly soaked being a less effective trap than one merely moistened with a few drops of the oil. The flies prefer the smell to be not too strong, but even when this is the case it seems to have a stupefying effect on them, making them dazed and lethargic, and quite impervious to ordinary alarms. A very effective trap for them is a clean kerosenetin nearly filled with water to which ten or twenty drops of citronella oil are added. The flies sit on the sides of the tin, now and then approaching the water; as they sit they get more and more stupid, and finish by falling into the water and getting drowned. This way of catching them is quite as effective as using citronella fly-papers, and cheaper. On one occasion I exposed a glass tube of half-inch bore and about three and a half feet long, inserted a piece of cotton-wool wet with citronella at one end and corked it, leaving the other end open. Seven zonatus entered the narrow mouth of the tube and there remained until they died, sitting in a line with their heads toward the closed end of the tube.

When in the neighbourhood of citronella the flies sit or move here and there with wings expanded, often quickly extending the proboscis, and now and then cleaning the head with the fore-legs and rubbing them together. Not infrequently they stand and rock their bodies to and fro, a movement which seems to be associated with "court-

ship" in all species of Dacus that occur at Pusa.

On two occasions a number of males and females have been confined together in order to see whether the citronella smell would induce copulation, but without success. Too much importance must not be attached to this result, however, as the conditions were abnormal, and I have never succeeded in getting D. zonatus to copulate in the laboratory. These observations afford at least another argument that the olfactory sense of Diptera, or at any rate of D. zonatus, is not dissimilar in kind from our own: smells which in us give rise to similar sensations (i. e. citronella and \mathcal{L} zonatus) affect the male zonatus in the same way, though its perception of them is far keener than ours.

Among well-known instances of attraction by smells resembling the food of the larva or adult is the case of certain evil-smelling Aroids which are attractive to various flies and beetles accustomed to infest putrescent matter. It has been found that a mixture of certain proportions of acetic acid and ethyl alcohol is most attractive to Drosophila ampelophila, whose larvae live in over-ripe fruit. Similarly, I have myself observed Sarcophaga to be very strongly attracted by a flask containing a solution of skatol, a substance normally present in faeces; many larvae were laid in the flask and were drowned in the The same fate attended the eggs of Stomoxys calcitrans which I have obtained in numbers on cottonwool soaked in valerianic acid, one of the acids present in the fermenting vegetable stuff in which the eggs of this species are naturally deposited; both valerianic and butyric acids have a similar attraction for an Ortalid fly of the genus *Ulidia* (?) which is not uncommon at Pusa.

Our own sense of smell seems to be practically limited to substances having a molecular weight of about 30 or over; those with molecular weight less than this have no smell or only a very faint one, though they may have an irritant effect on the mucous membrane of the nose. The fact that house-flies will suck freely a dilute solution of formaldehyde (mol. wt. 30) may perhaps indicate that their sense is limited in the same way (Alex. Hill, Nature). I have found that they will sometimes take a solution of hydrocyanic acid (mol. wt. 27), and this might be regarded as evidence supporting this supposition.

Another suggestion is that the olfactory sense of flies may be highly developed in certain directions and within certain narrow limits, while outside these limits it is comparatively inoperative. We should on this hypothesis expect to find instances where the males were very sensitive to the smell of the females or vice versa, the sensitiveness being, however, probably confined to one sex; the smell of the feod of the adult fly would attract both sexes if they fed on the same substances, while the food of the larva would, by its smell, direct the female in oviposition. Other smells, unless very strong, would have little effect.

Regarding the matter as thus crudely put, we might look on each species as tuned to respond to three or four notes on the scale of smell, and we should expect to find the most delicate adjustment and most accurate "tuning" in the direction of the sexual smell, since errors of perception would here be most disadvantageous to the species. There would be a correlation between the degree of specialisation of the larva in the matter of diet and the definiteness of the smell which would prompt the female to lay eggs. In many cases the food-smell of the adult fly would be least narrowly adjusted. At all times other senses such as those of sight and touch might play a more

or less important part as auxiliaries or controls.

If we accept for the moment some such view as this, then among those species in which the male finds the female by smell we must regard each one as an assemblage of individuals in which one sex is tuned to respond to a certain definite kind of molecular vibration corresponding to some compound or mixture of compounds emitted by the other sex, and these compounds would thus constitute definite specific characters. We might even perhaps go further and define some of the larger groups by those "generic" smells which characterise certain kinds of chemical substances, such, for instance, as the organic acids, the alcohols, amines, terpenes, etc., and which depend on the presence of certain atoms or of atomic groups of some particular configuration.

In any case it seems a very remarkable fact that two species such as *D. zonatus* and *D. diversus* which live in the same district, and have always been regarded as quite distinct, should have exactly the same sexual smell. There is, of course, the possibility that citronella does not repre-

sent the sexual smell, but owes its attractions to some other cause: the proof is at present incomplete. There remain at least two other solutions of the difficulty. One is that the samples of citronella used contained two or more active ingredients which appealed respectively to zonatus and diversus, and the other is that zonatus and diversus are not really distinct species at all, but varieties. I hope to be able to give further attention to these points.

If my conclusions are correct regarding the nature of the phenomena, they afford an interesting example of the imitation by artificial means of a sexual attraction probably similar in kind to that which operates in most cases of "assembling." It has occurred to me as possible that the curious predilection of another fruit-fly (*Ceratitis capitata*) for kerosene oil might perhaps be explained in the same way, but I do not remember to have seen any record of the relative numbers of males and females captured by this method.

EXPLANATION OF PLATES XXXIX, XL.

PLATE XXXIX. Males of Dacus zonatus attracted to handkerchief moistened with oil of citronella.

PLATE XL. The same three minutes after the flies had been dispersed.